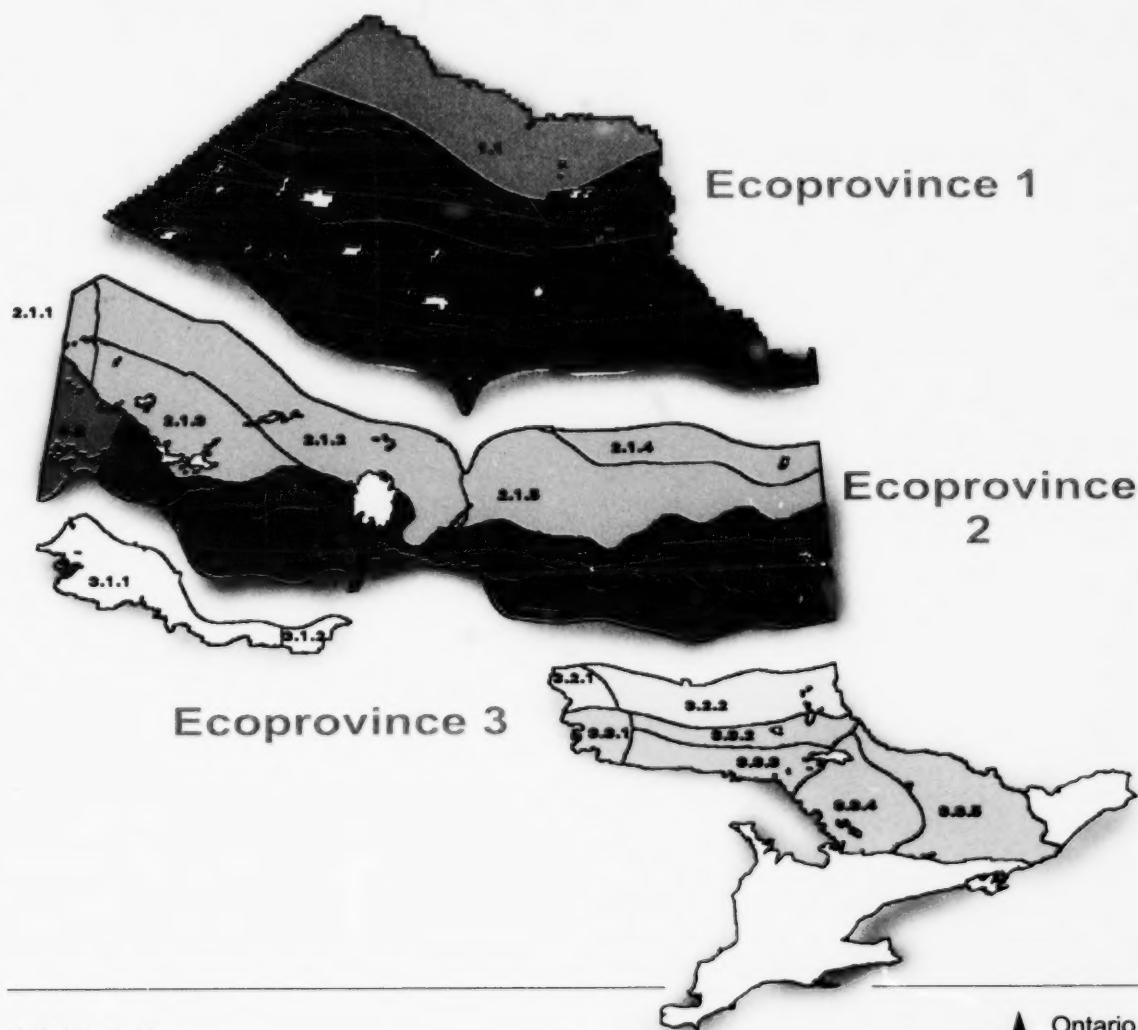


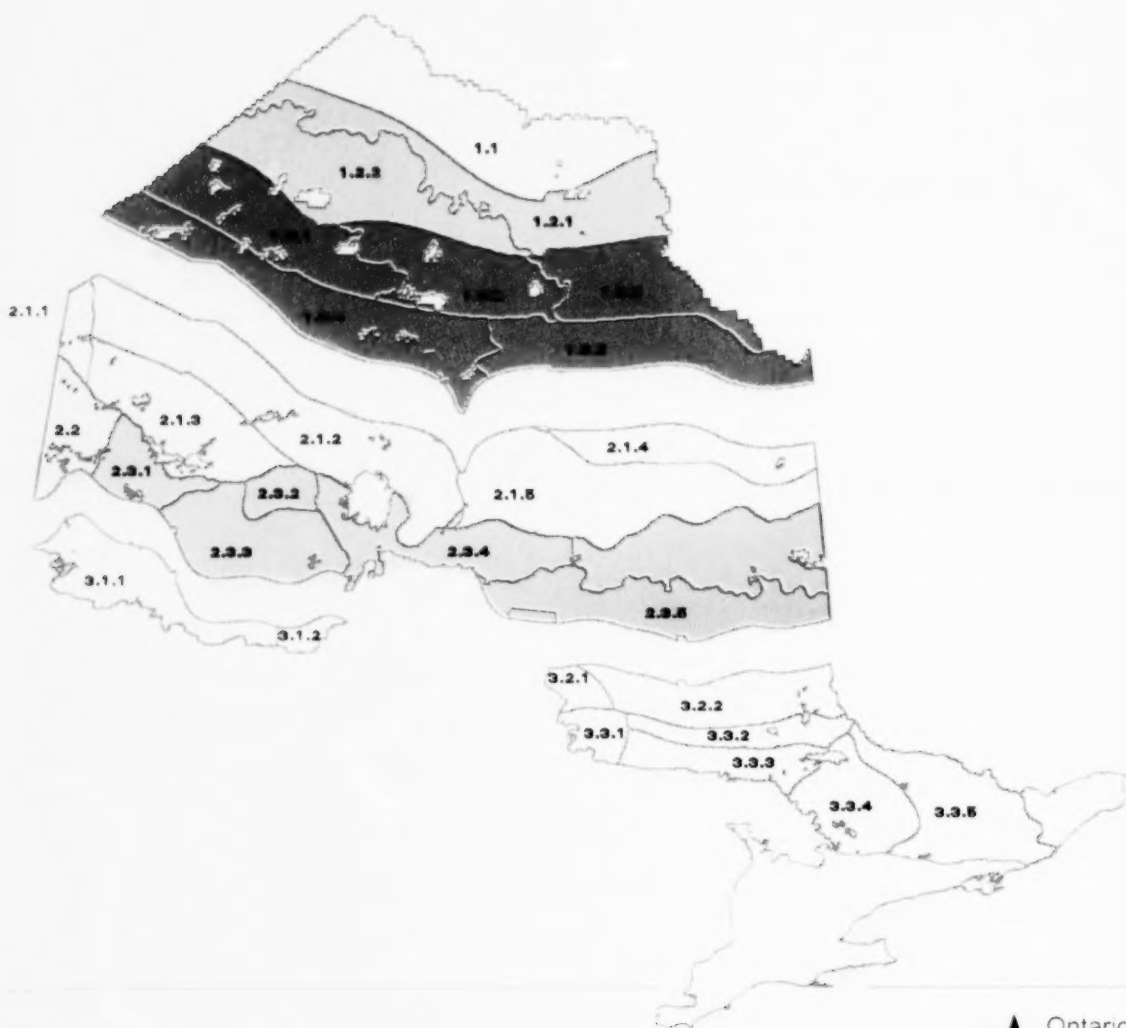
Deriving an Eco-regional Framework for Ontario

Through Large-scale Estimates of Net Primary Productivity



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by

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May 1999

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P6A 2E5

Canadian Cataloguing in Publication Data

Deriving an eco-regional framework for Ontario through large-scale estimates of net primary productivity

(Forest research report, ISSN 0381-3924 ; no. 149)

Includes bibliographical references.

ISBN 0-7778-8796-7

1. Ecosystem management—Ontario.

I. Band, Larry E. (Lawrence E.).

II. Ontario Forest Research Institute.

III. Series

QH77.C3D47 1999 577'.09713 C99-964011-9

© 1999, Queen's Printer for Ontario

Printed in Ontario, Canada

Single copies of this publication
are available from the address
noted below.

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Abstract

The Hierarchical Ecological Framework (HEF) project was initiated by the Ontario Ministry of Natural Resources to provide a hierarchical framework for understanding and managing the ecosystems of Ontario. The focus of this study was to estimate the distribution of ecosystem productivity at the provincial scale and to explain the nested patterns of productivity based on geoclimatic variables. This work serves as the first in a series of successively nested investigations into the controls and spatial patterns of forest ecosystem processes. The approach uses advanced technologies in remote sensing, geographic information systems, hydroecological simulation modelling, and spatial statistical analysis. At the largest spatial scales (ecoprovince to ecoregion), geoclimatic controls explain much of the variance in productivity across the province. At progressively smaller spatial scales (ecodistricts), local landforms and soils control productivity. The techniques developed were used to partition Ontario into distinct, ecologically consistent, nested zones. This partitioning framework has certain similarities to and advantages over more commonly used ecological regionalization systems and provides a flexible analytical toolbox with many potential applications.

Acknowledgements

This project was funded by the OMNR through Environmental Assessment Act Term and Condition 107 (a) to the Forest Landscape Ecology Program of the Ontario Forest Research Institute. We thank David Baldwin, Lisa Buse, Maureen Elgie, Abby Obenchain, and Terry Taylor of the Ontario Forest Research Institute for their assistance.

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INTRODUCTION

The Hierarchical Ecological Framework (HEF) is a collaborative interdisciplinary project initiated by the Ontario Ministry of Natural Resources (OMNR). HEF is designed to stratify the spatial heterogeneity of geoclimatic characteristics in Ontario in support of sustainable resource management. The key features of this framework are outlined in Perera et al. (1996).

HEF focuses on terrestrial heterogeneity and complements marine and other ecosystem classification schemes. It is based on hierarchy theory, i.e., the ecosystems are functionally and spatially nested. HEF uses the terminology of the Canadian Committee on Ecological Land Classification (*ecoprovince*, *ecoregion*, *ecodistrict*, *ecosection*, and *ecosite*) (Wiken 1979). It defines systems from top down (from *ecoprovince* to *ecodistrict*) and allows for developing *ecosections* in conjunction with Ontario's Forest Ecosystem Classification system, which will develop *ecosites* and *ecoelements*. This report describes the nested system of *ecoprovinces*, *ecoregions*, and *ecodistricts* that was derived by analyzing spatial patterns of vegetation cover productivity in relation to geoclimatic, landform, and soil variation across Ontario. Emphasis is placed on explaining and demonstrating the methodology.

According to hierarchy theory, the patterns and functioning of each level are explained by the mechanisms operable at the next lower level. In this investigation, the patterns, functions, and processes composing this inter-scale feedback were analyzed based on both biophysical principles and the climate, geological, topographical, and disturbance factors dominant at different scales. To quantify as well as classify ecosystem processes, net ecosystem productivity was used as a basic variable to characterize forest ecosystem function. At each scale, the supports and constraints of characteristic regional productivity were determined. Ecosystem

productivity was a central and basic variable because of its direct links to forest renewal, growth, trophic chain, and the atmospheric carbon budget processes. In addition, it links indirectly to the formation of the landscape mosaic and to hydrologic processes of evapotranspiration, runoff, and sedimentation.

The goals of this investigation were to:

1. Produce an estimate of forest net canopy productivity, measured as the net assimilation of carbon by the canopy, in mass of carbon per unit area, at coarse spatial resolution appropriate to *ecoprovince* to *ecodistrict* analysis.
2. Investigate the abiotic controls of forest productivity (climate, landform, and soils) and their variation across the province.
3. Use the spatial patterns of estimated forest productivity along with the set of controlling geoclimatic variables to partition the province into a set of polygons at the *ecoprovince*, *ecoregion*, and *ecodistrict* scales. The methodology for this nested partitioning should be objective and provide:
 - a) Contiguous regions
 - b) Clear, reproducible reasoning for each polygon, including controlling abiotic variables
 - c) Quantification of the "strength" of the boundary lines defining the polygon.
4. Investigate the spatial patterns (degree of surface heterogeneity) of forest productivity across Ontario. Understanding the degree of homogeneity or heterogeneity is required to assess the impact of forest policies and management practices and to allocate resources for collecting basic information.

To achieve these objectives, the following steps were taken:

1. The Regional HydroEcological Simulation System (RHESSys) was used to estimate forest

ecosystem processes at high resolution across a range of Ontario landscapes.

2. The results were used to calibrate a coarse-resolution, satellite-driven method for estimating forest productivity and evapotranspiration across the province.
3. Using the hierarchical techniques of regression trees, the estimated provincial forest productivity was combined with GIS data sets characterizing long-term climate patterns and terrain and substrate information to extract a statistical explanation and a regionalization of the dominant controls of forest productivity.
4. Using an adaptive, divisive, image-processing technique derived from quadtree, the dominance of control of forest productivity by geoclimatic variables was investigated. Quadtree structure was used to describe scaling behaviour, expressed as the heterogeneity and diversity of the province's forest ecosystems over a range of scales.

METHODS

Productivity in Ontario is primarily estimated using RHESSys with coarse-level satellite data to simulate a spatially distributed ecosystem. RHESSys has been used successfully to predict watershed hydroecological processes, including the distribution of forest growth and hydrology in a set of experimental forests and watersheds (Band 1993a, 1993b, Creed et al. 1996, Mackay and Band 1997). RHESSys has also been used to estimate ecosystem productivity for 1 growing season at the ecozone scale including the full province and portions of adjacent provinces and states (Band 1995). The Advanced Very High Resolution Radiometer (AVHRR) Pathfinder data set (Agbu and James 1994) at 8 km x 8 km resolution was used to estimate fractional canopy absorbed photosynthetically active radiation (FPAR). FPAR has been shown to scale approximately linearly with the Normalized Difference Vegetation Index (NDVI), which is routinely

produced as part of the Pathfinder data set for the full globe. Combining estimates of incident PAR with FPAR produces the absorbed PAR (APAR), which correlates linearly with net canopy productivity (NPP) (Monteith 1977) as:

$$NPP = \epsilon * APAR$$

where ϵ is the constant of proportionality, or radiation conversion efficiency, expressed here as grams of carbon assimilated (above- and belowground minus the respiration losses) per megajoule APAR. ϵ must be estimated at landscape scales commensurate with the sampling resolution of the Pathfinder data set. In the current study, RHESSys was used to simulate (among other processes) the absorption of PAR and net assimilation of carbon over a set of representative landscapes. Averaging these processes over areas sufficient to be discriminated by the AVHRR provided landscape average values at scales commensurate with the satellite-driven analysis used in the nested levels (ecoprovince to ecodistrict) of HEF.

Using RHESSys

RHESSys is a spatial data processing and simulation system designed to predict and assess forest ecosystem processes at the landscape level (Band et al. 1993, Nemani et al. 1993). RHESSys explicitly uses the patterns of soil, landform, terrain, forest canopy properties, and micrometeorology to estimate the distribution of carbon, water, energy, and nutrient budgets over the landscape. Figure 1 shows the basic structure of the system, including the spatial and temporal data sets required as inputs; the intermediate GIS processing of these data into a set of model input variables and parameters; the biophysical simulation models that compute carbon, water, energy, and nutrient flux processes; and the primary model outputs.

RHESSys works by estimating and spatially organizing the information required to compute a set of driving meteorological variables and the resistance to vapour and carbon exchange

RHESSys

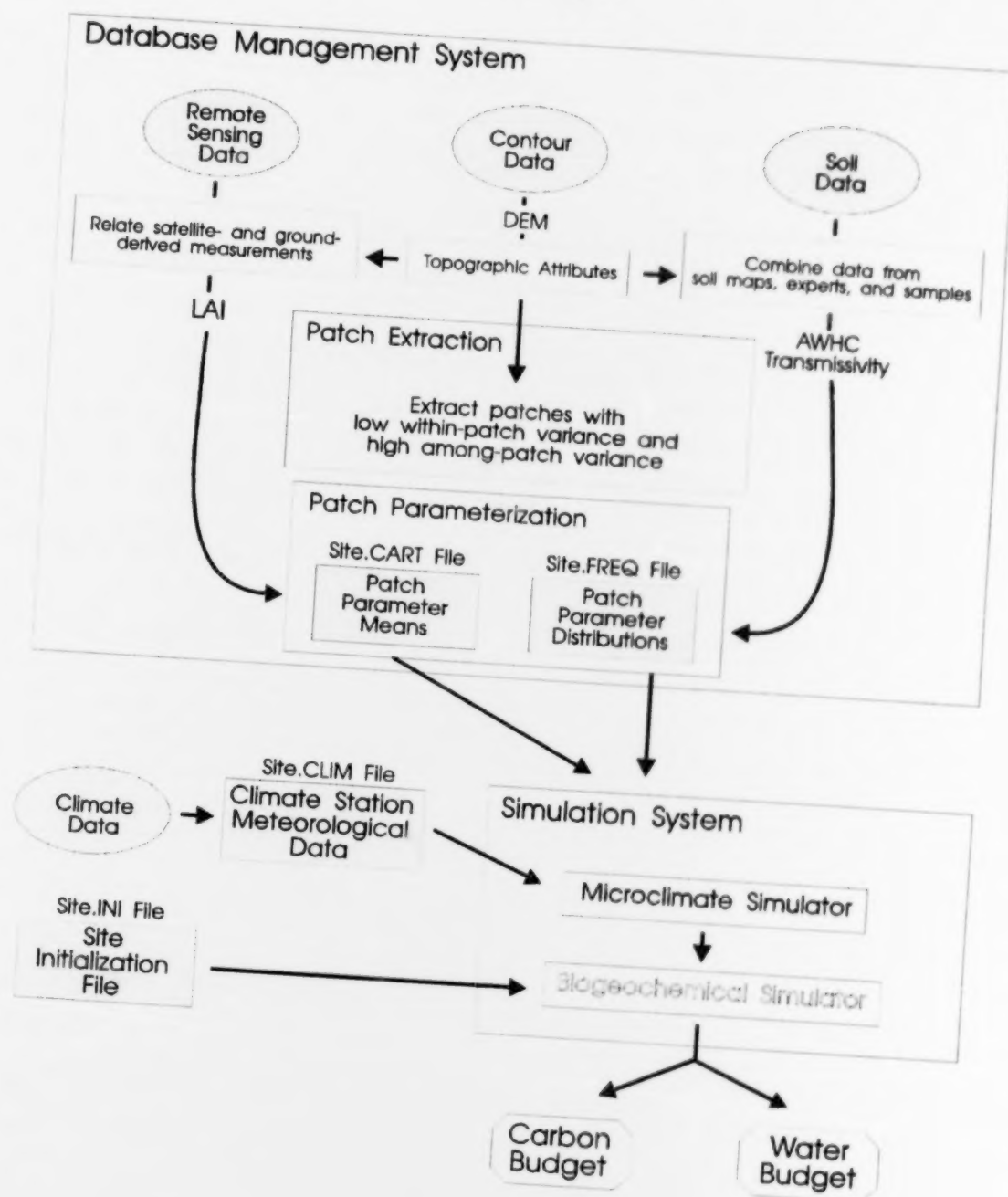


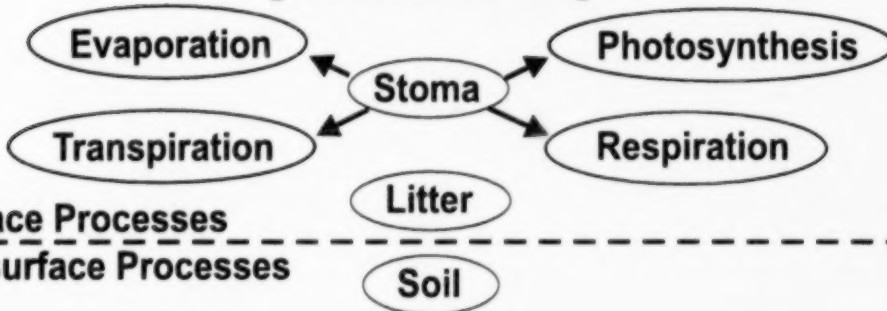
Figure 1. Flow diagram of RHESSys, including spatial data processing, parameter estimation and input file structure, biogeochemical models, and simulation output.

Simulation System

Microclimate Simulator
[MTCLIM]



Biogeochemical Simulator
[FOREST-BGC]



Hydrological Simulator
[TOPMODEL]

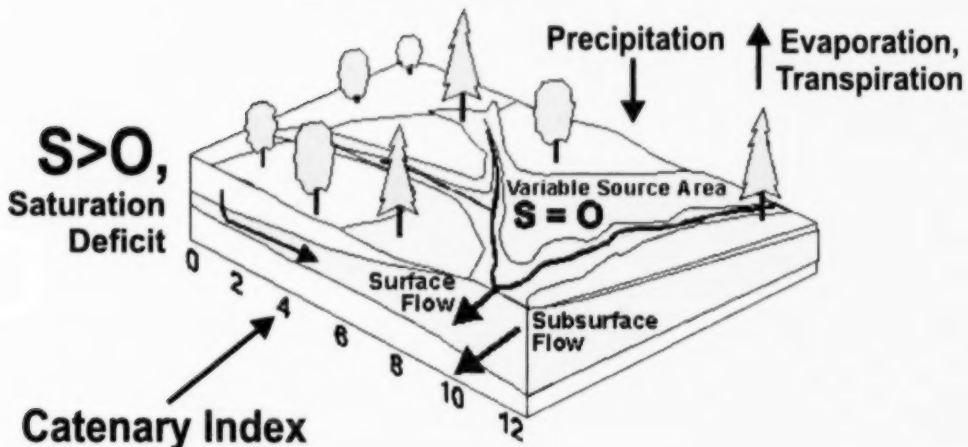


Figure 2. Details of biogeochemical model integration of MT-CLIM, FOREST-BGC and TOPMODEL. Main processes of water and carbon flux are represented.

offered by the ecosystem. Stomatal resistance is modelled as an empirical function of temperature, the vapour pressure deficit, PAR, and the available water content of the soil in the root zone. A microclimate extrapolation method is used in combination with a watershed hydrology model to simulate distributed soil water. Thus, the important assumption that drives RHESSys is identifying the primary abiotic and biotic controls of forest ecosystem processes within specific landscapes and then finding efficient ways to measure and represent the patterns of these factors over the landscape. The spatial data processing portion of RHESSys performs this function.

In a given landscape, the mix of specific forest life forms and topographic structure explains much of the variance in forest productivity. These patterns result from a combination of geomorphic and disturbance history, coupled with the patterns of soil water and nutrient flows. In Ontario, we use either the terrain structure, given by the patterns of subcatchments and hill slopes in a watershed as determined by digital terrain analysis, or the set of remotely sensed forest stands to represent the landscape. The choice depends on the relative dominance of each pattern. Variation within hill slopes or forest patches are also incorporated.

In the current study, all processes were modelled with a daily time step because daily meteorological data was readily available. Longer time steps could miss or average out effects of nonlinear ecological and hydrological processes. The modelled processes include stand photosynthesis, respiration, evaporation, transpiration, and runoff production (Figure 2). For more details about these processes, see Band (1993a).

Simulating over an Ontario transect

Applying RHESSys to different landscapes in Ontario has been described by Band (1993a, 1993b) and Band et al. (1995). Comparisons of RHESSys model outputs with observed runoff production, forest growth, accumulated biomass

and snow depletion curves at sites near Petawawa and Sault Ste. Marie indicate that RHESSys reasonably approximates field conditions (Band 1993b, Creed et al. 1996, Mackay and Band 1997). Sites used as part of this gradient are the Petawawa National Forestry Institute, a site in the Temagami District of Central Ontario, the Turkey Lakes Experimental Watershed in the Algoma Highlands, and the Rinker Lake study site near Lake Nipigon (Figure 3). This transect provides a reasonable (albeit simple) gradient across Great Lakes/Laurentian land into the southern boreal biomes of the province; however, more sites are being added to provide a more representative sample of Ontario ecosystems.

The landscape-level simulations described above produced landscape-averaged estimates of the canopy APAR as well as the net canopy productivity, thus allowing the estimation of landscape average for each site along the Ontario transect.

Figure 4 shows the variation in the radiation conversion efficiency, ϵ , over the 1987 growing season for 3 of the sites along the transect. These curves represent areally averaged values for the full areas of each site. Each site varies greatly in ϵ at certain times of the growing season due to local edaphic and physiologic conditions at the stand level, but these local effects cannot be resolved at Pathfinder resolution or for the full provincial area. They are, however, very important to forming the areal average values, as the controlling factors can be very nonlinear (Band 1993a), and to resolving the landscape-level patterns of productivity at the ecoelement level.

Figure 4 also illustrates a rough progression of phenologies based on climatic and biome conditions, with the more boreal sites showing a delayed increase in ϵ during the spring and an earlier reduction in the late summer/early autumn. This reflects colder temperatures, and to an extent, more conifer lifeforms, which cannot make use of the absorbed PAR while temperatures are low. The higher values in the



Figure 3. Transect of 4 sites across Ontario used to operate RHESSys and calibrate AVHRR-based productivity estimates.

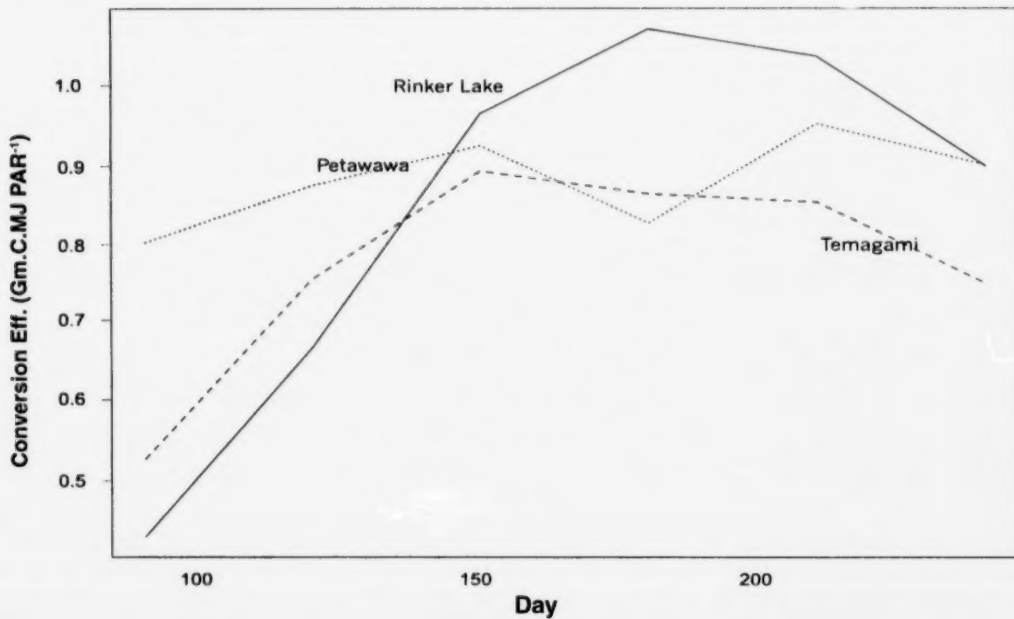


Figure 4. Monthly composited trajectories of the energy conversion efficiency factor for 3 of the 4 transect sites.

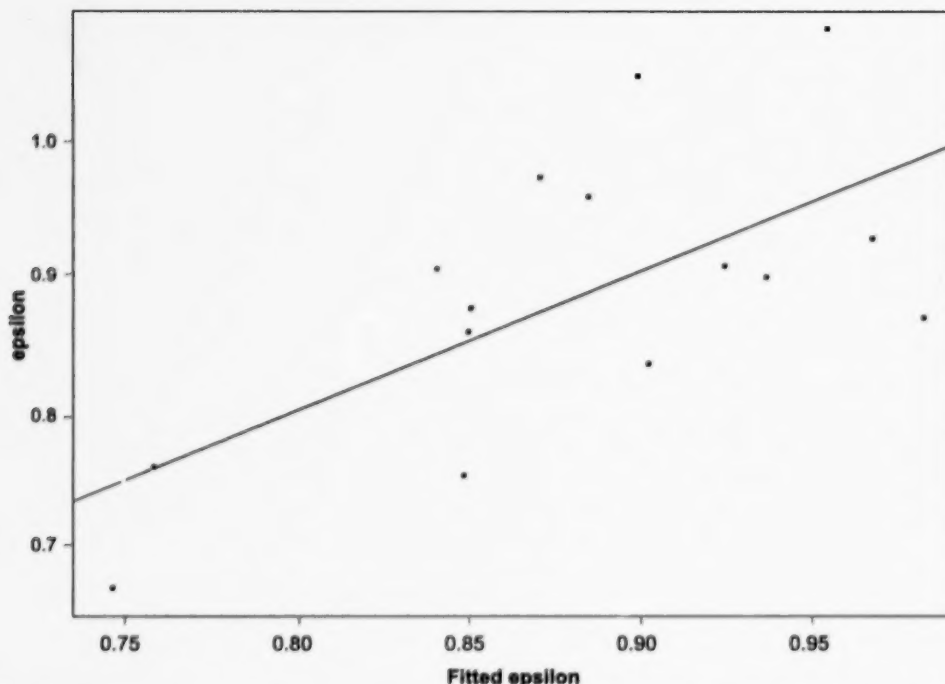


Figure 5. Mean monthly ϵ as simulated by RHESSys plotted against predicted ϵ as a function of mean monthly temperature and precipitation for the transect of landscapes across Ontario.

summer for the southern boreal site may reflect a more favourable water balance with more surface water. This apparent increase in as mean annual temperature drops has also been noted by Landsberg et al. (1996). However, results from the BOREAS project have shown that despite abundant surface water in the canopy rooting zone, boreal canopies maintain low productivity due to stomatal closure at high vapour pressure deficit. The major drivers of the seasonal variations in are temperature limitations and to a lesser extent water limitations. About 50% of the monthly variations of in the different sites can be explained by mean monthly temperature and monthly precipitation (Figure 5). A multiple regression model based on these 2 variables provides a simple way to extrapolate a long-term average over the full province using 30-year average monthly temperature and precipitation.

We have used a simple explanation of ϵ , generated from monthly aggregated values simulated over representative landscapes and combined with long-term average climate

variables to estimate long-term patterns of the efficiency factor. Extending the number of sites across a greater range of conditions and adding more variables may improve the statistical explanation of and is planned for the future.

Since the simulations used 1987 data, to be consistent with the satellite data, we evaluated whether the relative patterns of productivity are consistent with other years. The year 1987 was warm and dry, thus we compared it with 1992, which was unusually cold and wet across the province. Relative productivity shifted some between sites. For example, simulated productivity for the Petawawa site was about 5% less in 1987 than in 1992 because of greater water stress in the former year. Turkey Lakes, which is in a wetter zone on the eastern shore of Lake Superior, had 5% greater productivity in 1992 than in 1987. However, this shift is small compared to the regional differences of productivity in Ontario, which can exceed a 3-fold change and overshadow the small

differences caused by local lake influences. Thus, large-scale regional relative patterns are reasonably stable for ecoregionalization at the ecoprovincial to ecoregional levels and probably down to the ecodistrict level, although long-term stability should be investigated more thoroughly at the ecodistrict level, where local weather anomalies may be significant.

Calibrating productivity using coarse-resolution satellite data

Using RHESSys, ϵ was estimated. Then APAR was estimated by convolving incident PAR with the fraction of incident PAR absorbed by the canopy (FPAR). Both quantities were based on coarse-resolution satellite data. Several researchers have used information collected by the AVHRR to investigate the distribution of vegetation cover and productivity at continental to global scales (Prince 1991, Potter et al. 1993, Goward and Dye 1996). The AVHRR passes over the full globe twice daily, and the daytime overpass is used to produce the Normalized Difference Vegetation Index (NDVI), which scales nearly linearly with FPAR (Goward and Huemmerich 1992). In the current study, we used the first year of data (1987) to estimate forest productivity for the province.

Incident PAR is estimated as approximately 50% of the incident shortwave radiation. Radiation data from meteorological stations is very sparse in Ontario and is largely restricted to the south. A $1^\circ \times 1^\circ$ data set, distributed as part of the Pathfinder program (Darnell et al. 1992), was used to estimate provincial productivity. The original radiation data were interpolated to the 8-km Pathfinder data set using a moving average technique for the growing season (May to September) of 1987.

Calculating growing season productivity for 1987

Figure 6 shows the monthly composited NDVI for May to September 1987. Figure 7 shows the integrated forest canopy productivity

for the growing season of 1987, following Equation 1. Through the winter months, forest ecosystem net primary productivity is significantly affected by ecosystem respiration losses from soil organic decomposition, but forest canopy respiration losses are small enough that the active growing season net carbon exchange is a reasonable index of productivity. In 1987, the distribution of forest canopy (and other biome) productivity in the province ranged from near zero (but with very little area under $50\text{--}100 \text{ gm.m}^{-2}$) to approximately 600 gm.m^{-2} (when sampled at $8 \times 8 \text{ km}$ blocks). Large water bodies were not included in this analysis.

Productivity generally increased from north to south, following temperature as expected, except in the heavily disturbed urban and agricultural areas of southern Ontario. The region north of the tree line is demarcated by a shift to lower productivity as relatively undisturbed areas of northern boreal forest gives way to tundra. Peak productivity is restricted to central and southern Ontario near (and downwind) of the Great Lakes. The limits of disturbance (and of higher productivity) appear to be controlled geologically and topographically, with the heavily disturbed urban and agricultural area of southern Ontario extending to the border of the Canadian Shield. High-productivity areas extend around Georgian Bay and through Algonquin Park and surrounding areas into eastern Ontario, the North Shore of Lake Huron, the eastern shore of Lake Superior (Algoma Highlands), and more isolated areas of the Temagami District.

Analyzing provincial productivity patterns

Two methods were used to partition the province into a nested hierarchy based on different partition criteria: 1) a simple density slicing of the province into productivity classes, and 2) regression tree and quadtree methods, both recently developed for hierarchical systems. With both methods, the statistical variance of the full image or a sample was used

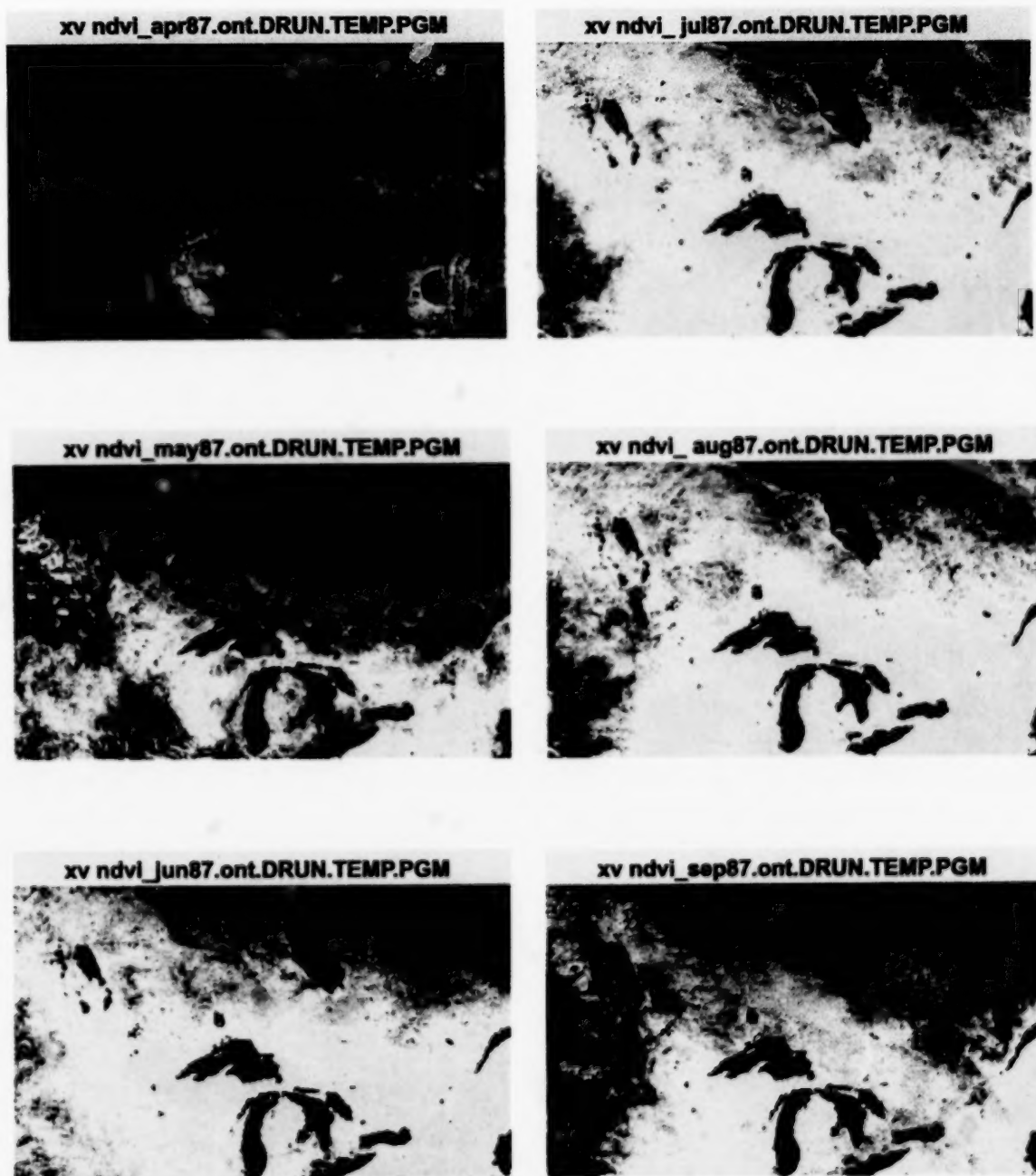


Figure 6. Monthly composited Pathfinder NDVI for April through September 1987.



Figure 7. Integrated forest productivity in gm.m^2 for the 1987 growing season in Ontario.

to guide a divisive technique that breaks the root image or sample into a set of successively nested subsamples. The regression tree uses a tree structure of successive sample splits to explain the variation in a response variable by a set of predictor variables. The quadtree decomposition repeatedly splits an image into 4 child cells until a stopping criteria of a threshold variance of the splitting variable is reached. (Note that references to *tree* and *leaf* indicate units of the quadtree and the regression tree, not forest components.)

The spatial partition produced by these methods was compared with 2 standard ecoregionalizations in Ontario: the Hills system (Hills 1961, Burger 1993) and the Ecoregions of Ontario (Wickware and Rubec 1989). These systems are based on manual and heuristic

consideration of ecological patterns, climate, and landform variables and are not quantitatively defined or designed to follow ecosystem productivity.

RESULTS

Density slicing of productivity

Prior to density slicing, the productivity surface was smoothed using a 25 x 25-km moving average filter. Smoothing largely eliminates local variance due to detailed terrain patterns and disturbance, emphasizing longer-range variability due to climate and physiographic/geologic structure. This representation of the productivity is consistent with the ecoprovincial to ecoregional

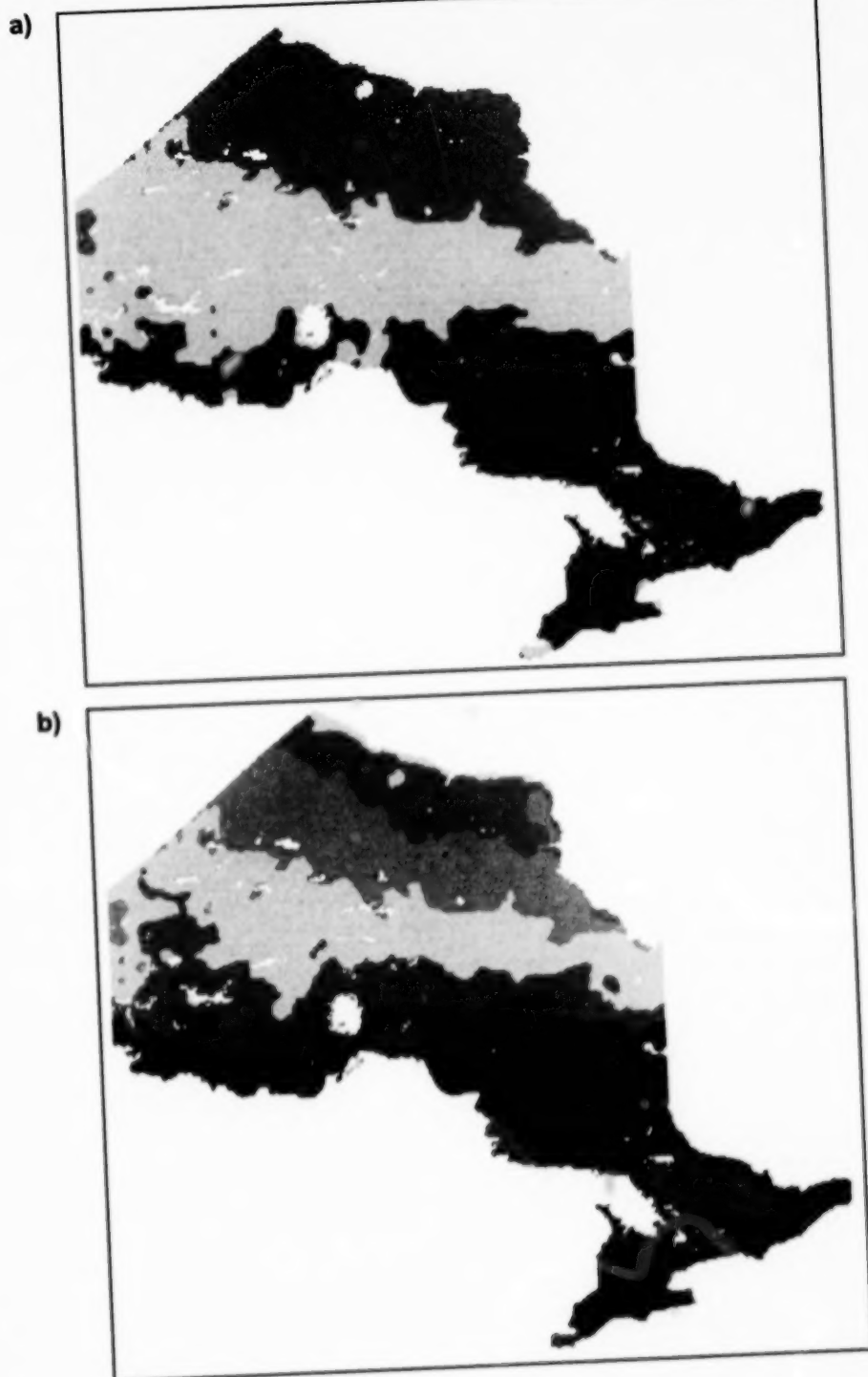


Figure 8. Density slice of forest productivity image smoothed with a 25 x 25 cell (200 km) window. Productivity classes are set equal to 100 gm.C.yr⁻¹ a) and 50 gm.C.yr⁻¹. b) productivity intervals from 0 to 600 gm.C.yr⁻¹.

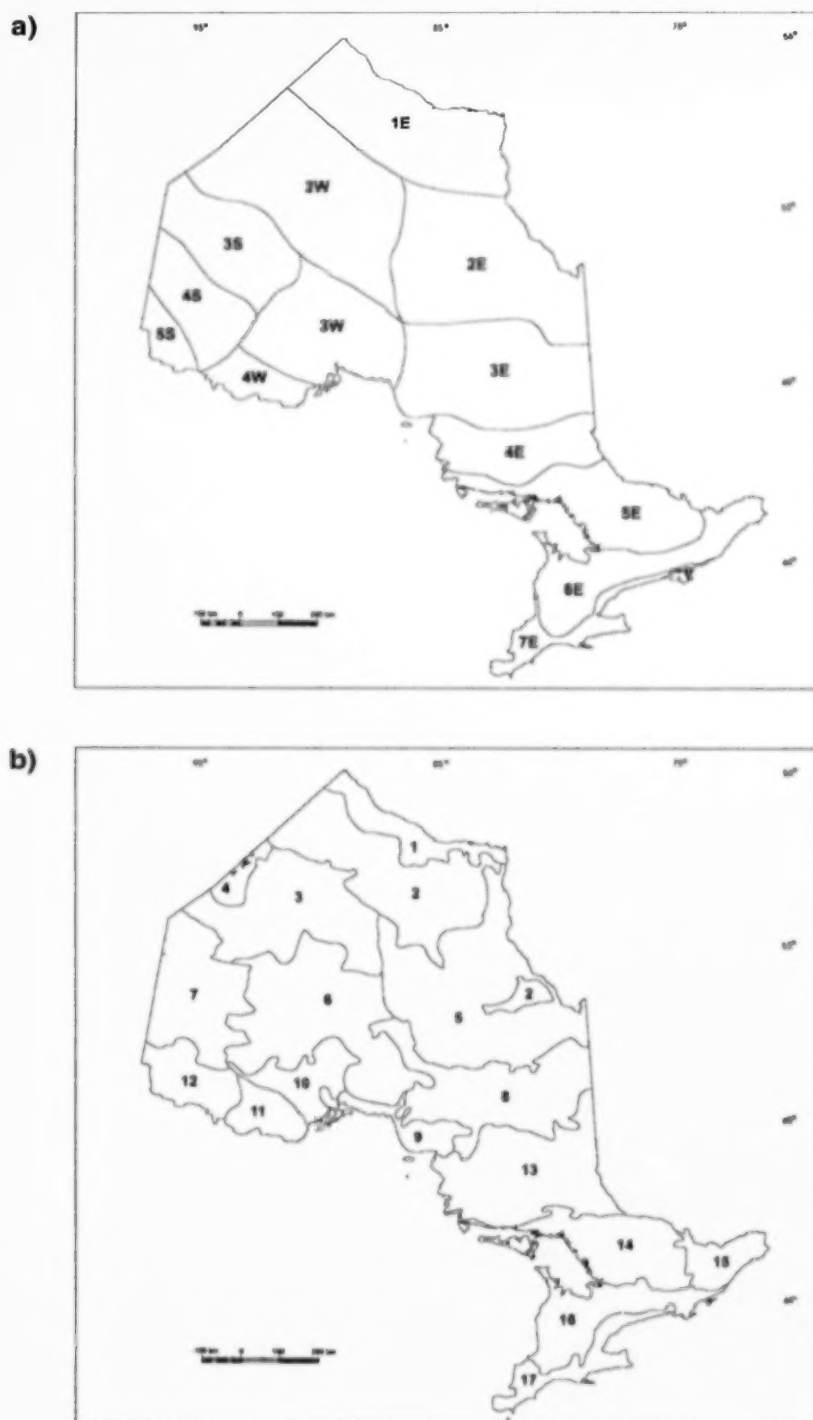


Figure 9. Eco-regionalization systems of Ontario: a) Hills, b) Wickware and Rubec.

component of HEF. Density (or histogram) slicing is a reclassification operation in which the population of a variable is classified into different ordinal units. One can choose equal-width intervals or create equal-size (or area) samples. We opted for the simpler method: choosing the number of classes desired and forming equal-interval classes. We then sliced the full range of 0 to 600 gm.m^{-2} into 100 gm.m^{-2} and 50 gm.m^{-2} class intervals (Figure 8a,b).

Density slicing of the smoothed Ontario productivity image produced a set of regions that has many similarities to the Hills (Figure 9a), and Wickware and Rubec (W&R) classifications (Figure 9b), reflecting both the distribution of forested regions and the variations due to temperature, physiography, and other abiotic factors. The W&R system is broadly similar to the Hills system, but it is more complex in its regionalization through northern Ontario, reflecting the availability and use of satellite information. Hills (1961) did try to order the controls on forest regionalization and stated that a prime factor was the climate "just beyond the local modifying irregularities of landform ... being modified only by major terrestrial features such as land and sea masses, mountains and broad plains." Some of the W&R boundaries show details of estimated productivity that are not as well captured by the Hills system, which uses smoother boundaries of estimated isotherms, isohyets, and (at lower levels of the hierarchy) physiography.

Although the productivity image, the density sliced productivity image, and the 2 ecoregional classifications have significant similarities, some differences cannot be rectified, reflecting their different methods and goals. It may be possible to "tune" the segmentation by choosing other class boundaries instead of the simple equal-interval method used here. However, tuning the boundaries of these classes to Hills or W&R regions may be arbitrary and does not illuminate the controls of productivity, although it was instructive to quantify the Hills and

W&R classification systems in terms of the variations in productivity between regions (Baldwin 1997). The density slicing also does not produce contiguous regions, as similar levels of productivity can be gained in different regions, but for different purposes. This inability violates the constraints for the ecoregionalization scheme outlined earlier. Finally, no association of regions is produced by density slicing with any of the controlling geoclimatic data fields.

Regression Tree analysis

A regression tree analysis was run to explain the variance in the distribution of forest productivity in Ontario at the scale of ecoprovinces to ecoregions. Regression trees are designed to iteratively divide statistical samples into a binary tree of subsamples that separate a response variable according to 1 or more predictor variables. The splitting predictor variable is the one that minimizes variability in the resulting subsamples. Thus different variables may be used to partition the data sets in different branches of the tree, creating a flexible, explicitly nested operation that finds the most unique subpopulations at different levels. This method responds well to thresholds in the predictor variables and interactions between predictor variables. The splitting process is recursively applied to each subsample until a preset stopping criteria is met or all subsamples are too small to separate statistically. The tree is then pruned back to a desired depth, based either on heuristic criteria or on efficiency optimization in terms of the residual variance and the number of leaves.

The regression tree as applied here is an aspatial statistical process. However, the strong autocorrelation of driving geoclimatic variables results in a statistical sample partitioning that is effectively a consistent spatial partitioning. The sample division method that is derived can be mapped by a set of logical statements regarding the predictor variables following the path along the tree to each leaf. For a more detailed discussion of regression tree analysis, see Efron

and Tibshirani (1991) and Breiman et al. (1984). Michaelson et al. (1994) used regression tree analysis to produce an ecological stratification of an area of prairie landscape guided by a satellite-derived vegetation index using a set of terrain and ground cover variables.

Predictor variables must be chosen carefully, although given an extended set of variables, the regression tree will choose those variables that explain the most sample variance for each split. One approach would be to use the set of predictor variables to which RHESys is most sensitive. However, RHESys acts at daily time steps and over much smaller scales than the full province. Given the ecoprovincial to ecodistrict extent for this phase of HEF, the resolution of the Pathfinder estimates of forest productivity, and the longer time steps required for representative estimates of forest productivity, we restricted ourselves to large-scale predictor variables appropriate for the ecoprovincial scale. These are:

- mean annual temperature (*annT*)
- mean annual precipitation (*annP*)
- elevation (*dems*)
- soil drainage class (*drn*)
- population density (*pop*)
- sea-level temperature (*sealT*)
- adiabatically adjusted temperature (*adiaT*)
- annual water deficit (*wdef*)
- standard deviation of elevation in a 21 x 21-km window (*sde*)

All variables were georegistered to a geodetic grid and sampled at a resolution of 34 seconds latitude and longitude to approximate the resolution of the original NDVI data. The climate variables were derived by spline interpolation of 30-year mean values from more than 300 meteorological stations in Ontario and adjacent jurisdictions. Interpolation was carried out with thin plate spline, using the algorithm *s.surf.tps* in the GRASS4.1 GIS package (CERL 1993). Three temperature variables were used to test what form of large-scale synoptic temperature or locally influenced adiabatic temperature patterns best explain the

productivity patterns at ecoprovincial to ecoregional levels. The terrain variables were derived from a 1 x 1-km resolution digital elevation model (DEM) for Ontario made available by the Ontario Ministry of Natural Resources (Mackey et al. 1994). For the scale of the present analysis, we smoothed the DEM with a 21 x 21-km moving average filter.

Although slope and aspect are terrain variables that may be expected to correlate with forest ecosystem productivity, the low resolution and the presence of artifacts produced by interpolation from contours preclude their effective use. Both *dems* and *sde* are indices of terrain complexity and landform. These indices are also a surrogate for basic geological structure as the combination of elevation and terrain complexity can distinguish between the major regions of the province (e.g., the Canadian Shield, Hudson Bay Lowlands). The soil drainage variable was derived from the Canadian Soil Information System (CANSIS), and ranged from *excessively well drained* to *very poorly drained*, and was transformed to an ordinal variable with a range of 1 to 9. The population density variable (compiled at the county level) came from 1990 census data and was projected to 1994 population estimates by the Global Demography Project at the United States National Center for Geographic Information Analysis. We have included it as a simple settlement disturbance index.

In general, the interpolated surface temperature field (not adjusting to sea level or for local adiabatic effects) was the most effective explanatory variable down to the ecoprovince level. At lower levels of the hierarchy, adiabatically adjusted temperature, precipitation, and then landform and soil variables contributed to partitioning.

Ecoprovinces

A sample of 5000 points across Ontario was generated using the simulated productivity and the 9 geoclimatic variables described above. The sampling method used a quadtree

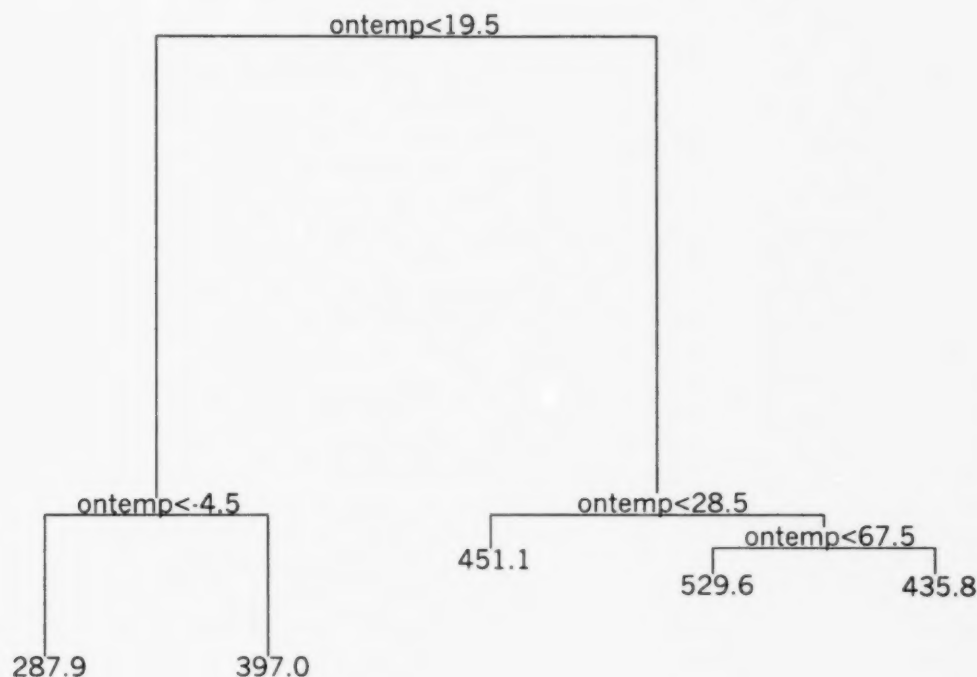


Figure 10. Regression tree structure for productivity as a function of geoclimatic variables with 5 leaves. Values of temperature are $\times 10$.

multivariate decomposition (Csillag and Kabos 1996) of the combined productivity and geoclimatic surfaces to stratify the density of points by spatial variance. This method produced a greater sampling density in more spatially heterogeneous areas. The regression tree constructed from this sample is shown down to a depth of 5 leaves with each node listed with the splitting variable and the mean productivity given at each of the leaves (Figure 10). The analysis shows that at the higher levels of the hierarchy, the climate variables (particularly *annt*) are the major source of variation in productivity. Terrain variables do not explain much of the variation until the lower levels of the hierarchy.

Table 1 shows the correlation matrix for a subset of climatic and landform variables, along with productivity, used for the regression tree. Figure 11 shows the residual sum of squares for the forest productivity at each level of the tree.

There are steep declines in residual sum of squares initially, from 1 to 2 leaves and from 2 to 3 leaves. This result indicates that at the highest levels, 3 leaves form an efficient set of ecoregions. Additional partitioning of the province with these variables reduces the residual variance only marginally using the regression tree. The structure of the partitions

Table 1. Correlation matrix for a subset of the geoclimatic variables and productivity showing strong spatial covariation of the suite of biogeoclimatic variables in Ontario.

	PSN	dem	temp	precip	drainage
PSN	1.0	.50	.73	.69	-.54
dem	.50	1.0	.41	.25	-.70
temp	.73	.41	1.0	.78	-.56
precip	.69	.25	.78	1.0	-.37
drainage	-.54	-.70	-.56	-.37	1.0

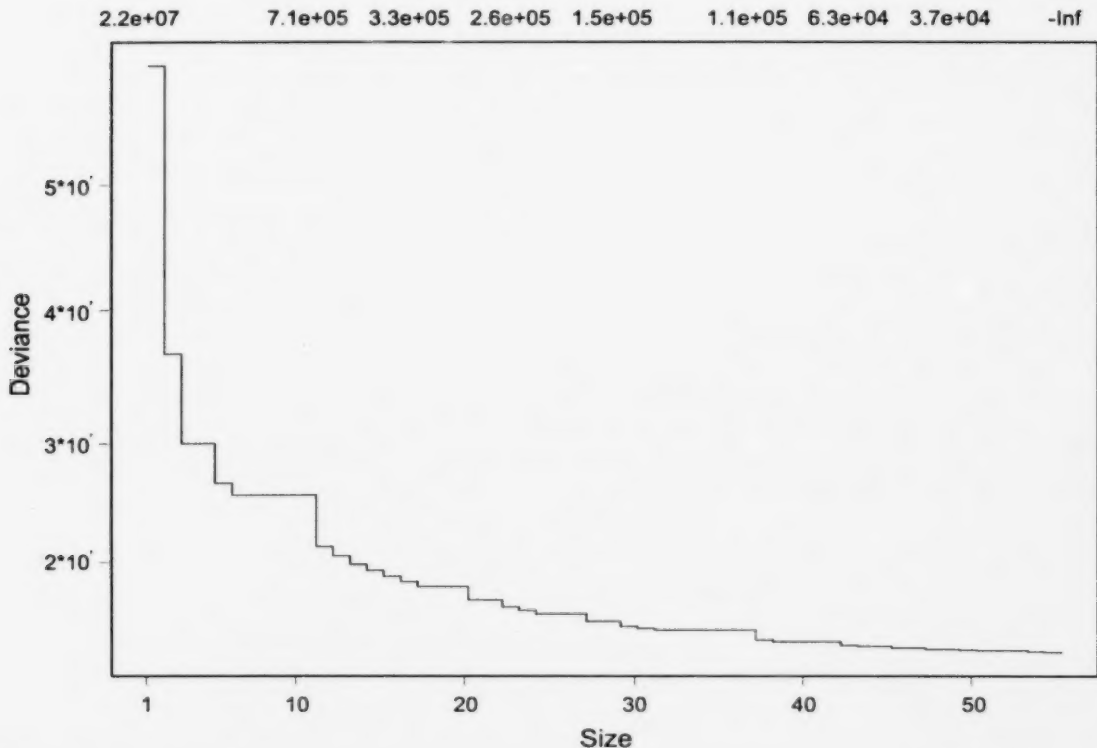


Figure 11. Residual squared deviations at different levels of the regression tree. The large drops from 1 to 2, from 2 to 3 followed by significantly lower drops, indicate an initial ecoregionalization into 3 ecoprovinces is justified. Approximately 50% of the total variance is accounted for by simple, 3 ecoprovincial-level split, with much of remainder due to high variance in southern Ontario.

(ecoprovinces) at the leaf level are shown in Figure 12a. The mean productivity within each of the ecoprovinces is shown in Figure 12b. A histogram of residuals of the 5-leaf regression tree predicted (using the mean productivity in each leaf) with the simulated Ontario productivity (Figure 13) shows that most of the province is well represented by the regression tree analysis. The major outliers cluster in southern Ontario, where disturbance is an overriding factor, and along some of the shorelines of the Great Lakes and Hudson Bay, due to some small registration problems and mixed land/water pixels.

Ecoregions

For each of the 3 ecoprovinces, a nested partitioning was accomplished by finding the 3

most distinct regions. The regression trees run for each ecoprovince showed a shift in the controlling variables to incorporate annual precipitation and adiabatically adjusted temperature surfaces, the latter showing greater local control (Figure 14a,b,c). In the southern ecoprovince, soil types or population are still not controlling variables, possibly due to the correlation of local temperature and terrain-based adiabatic adjustments to settlement and land-use patterns. At levels below ecoregions, the regression trees do partition with these variables. The ecoregion maps with mean productivity colour-coded are shown in Figure 15.

One of the ecoregions in the southern ecoprovince extends from Toronto through the agricultural area of southwestern Ontario, rather than splitting at the geological boundary of the

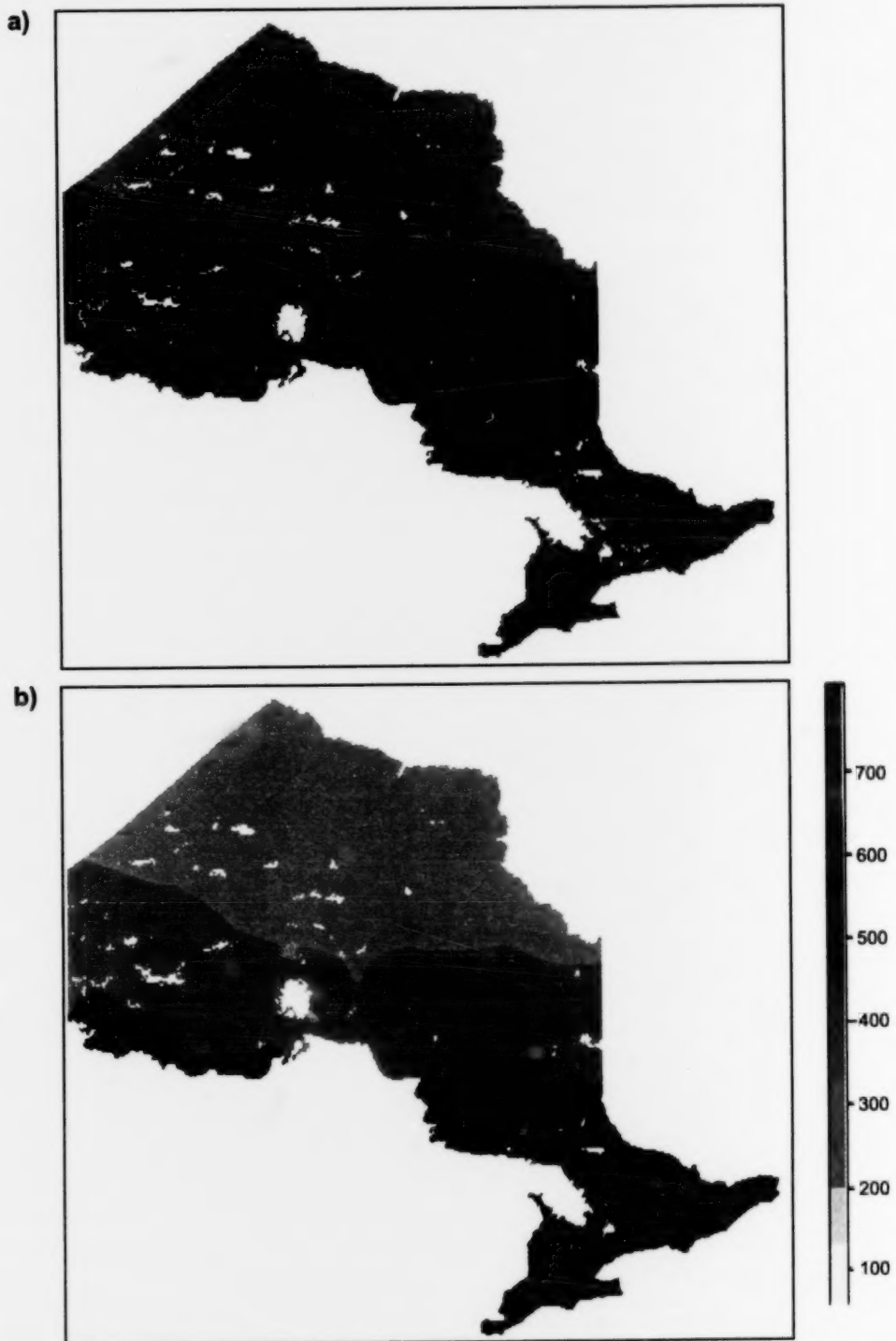


Figure 12. a) Regression tree-based partitions mapped back from regression tree splitting criteria for the geoclimatic variables for the 3 ecoprovincial regions. b) Mean productivity for the 3-(ecoprovince) leaf regression tree.

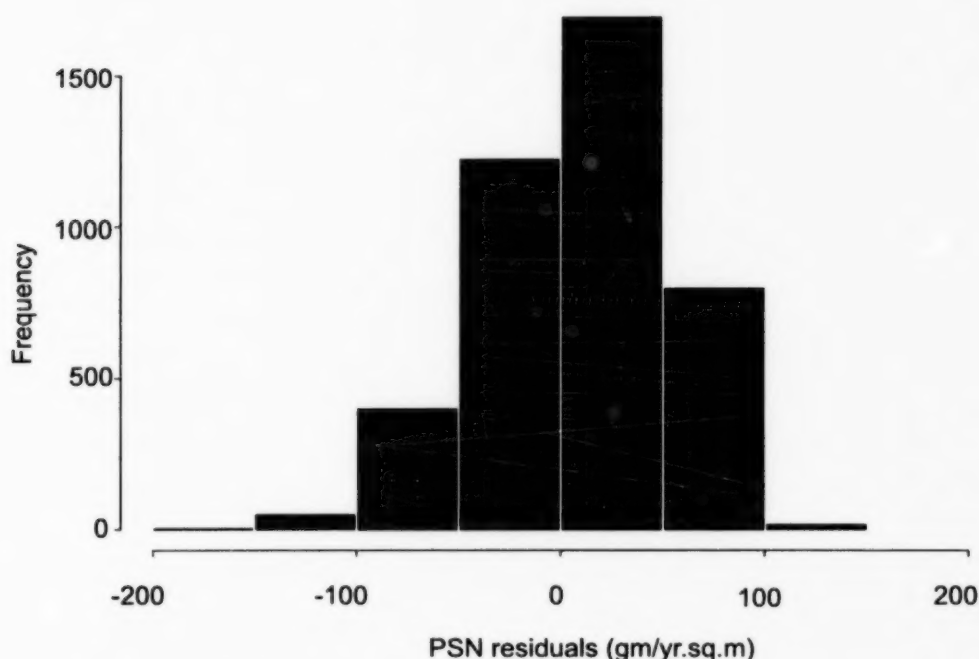


Figure 13. Histogram of residuals of the regression tree-based estimates of productivity from the simulated image of productivity. The full range of near zero to more than $600 \text{ gm.m}^2.\text{yr}^{-1}$ is well explained by simple, 3-region split with very little area having residuals greater than $\pm 100 \text{ gm.m}^2.\text{yr}^{-1}$.

Shield. The mixed productive agricultural and wooded areas of southeastern Ontario and the forest area north of the Shield boundary are similar in productivity. The focus of this investigation is on forested areas, thus boundary of the southern ecoprovince was adjusted to the south of the Shield, using a boundary digitized from Chapman and Putnam (1966). Repartitioning the modified southern ecoprovince with regression tree analysis produced a different set of ecoregions which were used for the rest of the investigation.

Comparison with other ecoregionalizations

The importance of climatic variables at the ecoprovince and ecoregion levels is consistent with general observations of the distributions of forest cover and productivity that underly both the Hills and W&R ecoregional classifications. The Hills classification system has site regions

at scales equivalent to the ecoprovince that are largely separated by isotherms or isohyets, while site districts and other lower levels of the hierarchy are dependent on landform and terrain. Hills (1961) identified controlling variables at different scales, a point reiterated and reviewed by Bailey (1996). The regression tree partitions and the Hills classifications have many similar to nearly coincident boundaries formed by isotherms and isohyets. The fact that 2 very different approaches, one based on manual observation and heuristic identification/association of control variables (Hills system) and the other on satellite-based simulation of forest productivity and advanced analytical technologies, tends to reinforce the basis of both.

The method presented here also quantifies the forest productivity across the regions and the hierarchy of explanation provided by climate and landform-based variables. In

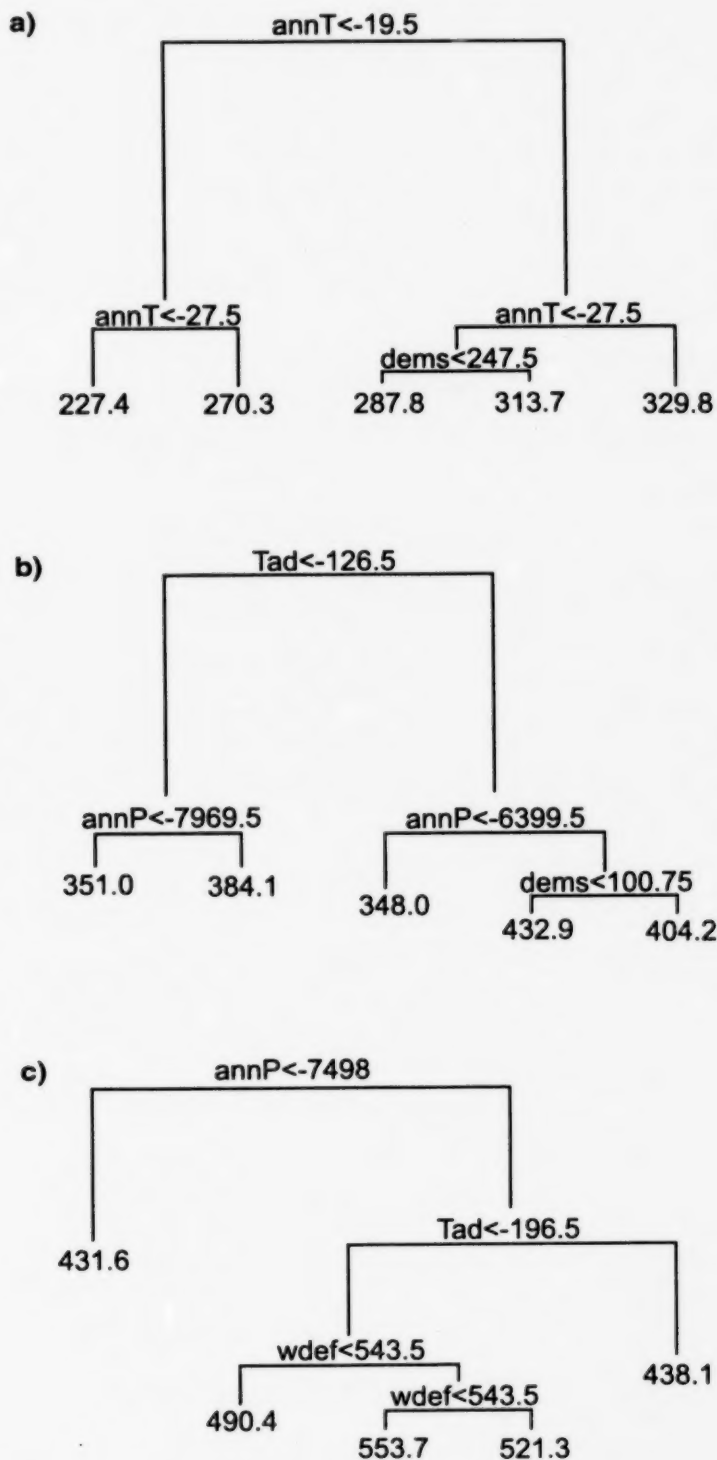


Figure 14. Regression tree structures for the a) northern, b) middle and c) southern ecoprovinces.



Figure 15. Mean productivity (gm.C.yr⁻¹) for each of the ecoregions, taken down to a level of the best 3 ecoregions in each of the ecoprovinces.



Figure 16. Image of productivity gradient (rate of change of productivity over space) computed with the smoothed PSN data set.

addition, it allows for the analysis of multi-year trends in forest productivity by extending to multiple years of satellite data. In the present analysis, 30-year mean annual climate variables were used. However, annual climate station data could be used to investigate variations in productivity due to climatic oscillations (e.g. El Nino, drought, and winter severity).

The W&R regionalization, which made some use of satellite imagery without ecosystem productivity as a dependent variable, has fewer similarities to the regression tree partitions. Wickware and Rubec used less uniform and explicit criteria and less constrained methods to create boundaries. The regression tree method creates simple ecoprovincial boundaries that follow isolines in one of the predictor variables that best separates the subsample at that location in the hierarchy. Using primary climate and landform data to determine the ecoprovinces and explain ecosystem

productivity produces boundaries that are isotherms, and further down the hierarchy, isohyets and terrain and substrate-related boundaries. The purpose and criteria for each boundary segment are explicitly shown, and are adaptable to regions with differing ecological limitations. The boundaries do not always correspond to zones of maximal rates of change of forest productivity, as the relative control of 1 variable at the ecoprovincial level can be modified by more local variables, such as topography or lake-induced precipitation effects. This is consistent with a hierarchical approach, as subregions of 2 parents regions can have similar productivity but different combinations of geoclimatic variables. In addition, the productivity image and its gradient (Figure 16) show that continuous high-gradient edges do not exist, due to the piecemeal, hierarchical variation of the set of controlling variables.



Figure 17. *Weighted similarity image of Ontario relative to the 3 ecoprovinces. Each cell is projected with green, blue or red with a weight proportional to the similarity of annual temperature to the control variable for this level of the regression tree (mean annual temperature) of each region. Gradational shift of similarity between regions shows "core" provinces and the rate of change relative to the control variable.*

Quantifying boundary strength

To show how ecosystem characteristics change across boundaries, we mapped the similarity of each cell to the *central concept* of each of the 3 ecoprovinces, using the control variable (temperature) rather than the response variable. Similarity weights were computed for each grid cell in the province relative to each of the ecoprovinces. These weights were calculated as the inverse of the normalized deviation of each cell's annual temperature to the mean annual temperature of each ecoregion normalized by computing a z-score. While the distributions of annual temperature were not gaussian, the difference in range of ecoregional temperatures required a normalization. The weights were then used to project colours as a composite image (Figure 17). In this scheme, the similarity image is closest to the colour of the ecoprovince it is most similar to and shows gradational degrees of similarity shifting between neighbouring ecoprovinces. This "fuzzy" rendition of the ecoregionalization has several advantages over the "crisp" boundary map.

In the full data set, terrain and substrate variables reduced variance only slightly; at lower levels, they were the primary source of variance reduction. This result is consistent with ecological hierarchy theory, which says that variables that determine system behaviour differ depending on the spatial scale.

Quadtree analysis

Quadtree analysis is a method of recursively partitioning images into a hierarchy of cells at successively higher resolutions down to a preset homogeneity (or heterogeneity) in a given variable(s) (Burrough 1986, Samet 1990). A quadtree decomposes the image starting from a full $2^n \times 2^n$ region into 4 child regions, repeating the decomposition in each child cell as long as a measure of within-region variance is exceeded. This decomposition results in a tree in which the terminal nodes, referred to as *leaves*, are below a preset variance threshold. Csillag (1997)

describes a method of using quadtrees to partition multivariate imagery beginning with arbitrary dimensions for environmental mapping and simulation. We adapted this method to partition the net canopy productivity fields estimated with the Pathfinder data over Ontario to determine which of the predictor variables match the scale of the response variable (net primary productivity).

This method yields an explicit hierarchy of regions based on the criteria of a level of ecological heterogeneity, which can be altered to produce a nested set of ecological units with successively greater levels of homogeneity. Regions of the province that show greater spatial variance of net forest canopy productivity can be partitioned to finer spatial detail to meet the need for more detailed (spatial) management strategies. From a policy standpoint, this knowledge aids in the allocation of resources for collecting new data and maintaining and managing different levels of spatial biodiversity. The level of quadtree decomposition in a region also serves as a simple index of landscape heterogeneity and diversity with the variables used, thus it can be used to quantify the heterogeneity and diversity of the landscape and ecosystem from an explicit hierarchy in terms of both variance and scale. For more details on the algorithmic implementation of the quadtree, see Csillag and Kabos (1996) and Csillag (1997).

Following the prescribed quad-based image decomposition, the subdivision and leaves must be square and therefore do not realistically regionalize the province's ecosystems into irregularly shaped polygons at higher levels of the tree (near the root). However, polygons can be formed by merging adjacent lower-level leaves based on similarity of the estimated mean forest productivity along with other driving variables. Alternatively, the quadtree analysis can be used to give the general location of regions, allowing the use of other criteria, including policy and management issues, to set precise boundaries.

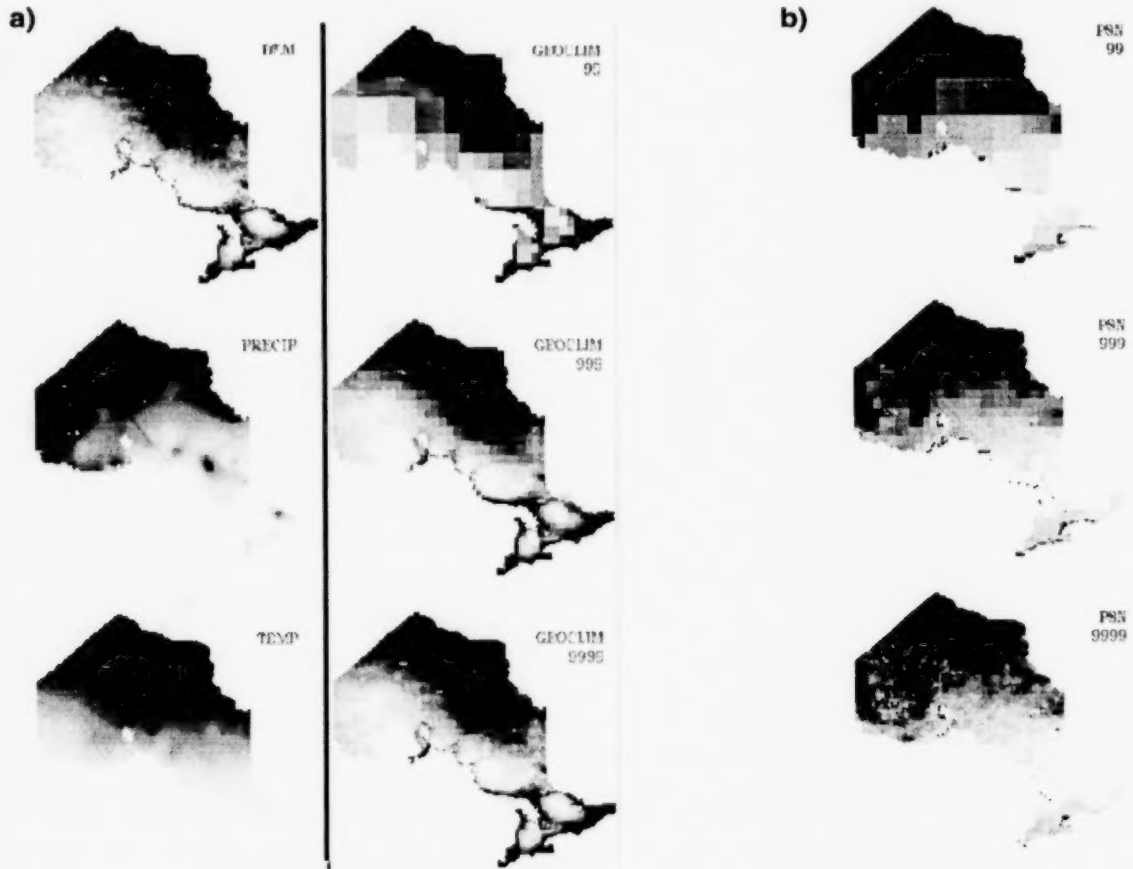


Figure 18. a) Surfaces of annual temperature, precipitation and elevation for Ontario with 3 levels of quadtree decomposition (99, 999 and 9999 leaves) for the geoclimatic variables. b) Three levels of quadtree decomposition for ecosystem productivity, with the same number of leaves as used for the geoclimatic variables.

For the current study, the quadtree analysis consisted of 2 decompositions to compare spatial diversity and patterns of the productivity surface with those of the set of geoclimatic predictor variables used in the regression tree analysis. We restricted our attention to *dem*, *annT*, and *annP*, as these were the only variables responsible for decomposition of the productivity data set in the first several splits. Figure 18a shows the original surfaces of *ontemp*, *ontpcr*, and *ontdem* for Ontario and a set of quadtree decompositions to different numbers of leaves. The leaves are shaded to the mean elevation, although at each level the splits

may be triggered by any of the 3 predictor variables exceeding a threshold variance.

Figure 18b shows the quadtree decompositions for the province using just the net productivity for the same number of leaves. The spatial decompositions of the geoclim and PSN (net canopy photosynthesis) surfaces did not coincide. Figure 19 compares the proportional reduction in the residual sum of squares as the quadtrees for the PSN and geoclimatic variables are decomposed. The climatic variables vary at regional spatial scales and thus tend to have longer length scales than

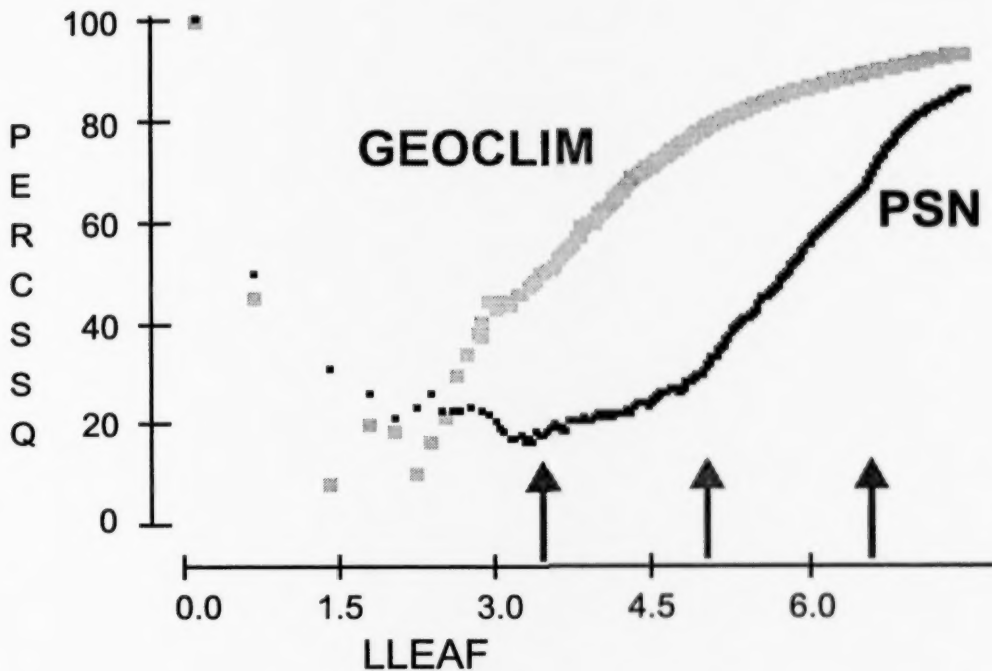


Figure 19. The proportional residual squared deviation for the productivity surface and the multivariate geoclimatic variable surface generated from the quadtree decomposition.

the productivity variable, which is more subject to local disturbance and the influence of landforms and soils. The productivity was estimated from an 8-km sampling of the surface, the climatic variables were smoothly interpolated from the meteorological station data, and elevation was interpolated from 1:250,000 contours.

Given the source and methods for forming geoclim variables, explaining productivity patterns by variation in the geoclim variables holds only for longer length scales or larger spatial scales of the ecoprovinces and ecoregions. At higher spatial resolutions, the information content of the specific geoclim variables increasingly diverged from that sampled for productivity using Pathfinder data. As we expanded our analysis to lower levels of the HEF hierarchy, the higher-resolution data sets became more important as predictor variables. We expected soil, topography (and

adiabatically adjusted climate), disturbance, and other land-based variables to become more important at the next level of ecoregionalization down to ecodistricts.

A further comparison of the spatial structure and scale of the geoclimatic and productivity variables can be seen in a plot of the leaf centres for quadtree decompositions with 999 leaves (Figure 20). In both decompositions, the greatest depth of the quadtree was reached along the coastlines of the Great Lakes and in Southern Ontario, although the productivity quadtree is much less evenly partitioned. This result may reflect the nonlinear and asymptotic controls of productivity by the abiotic geoclim variables. Temperature, precipitation, and elevation varied greatly in some parts of the province, whereas the 8-km estimated productivity varied little. Thus, simple linear models are unsuitable for predicting or characterizing productivity over the province.

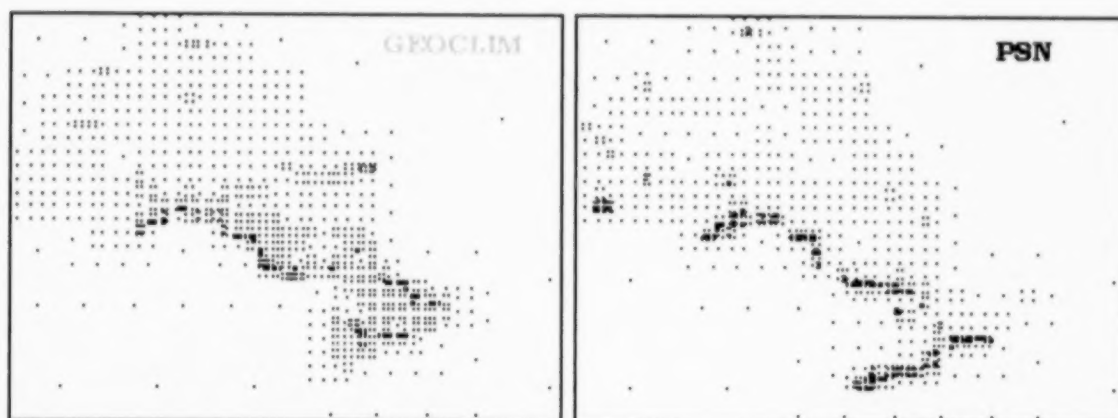


Figure 20. Leaf centres for the quadrees decomposed from the productivity and geoclimatic data.

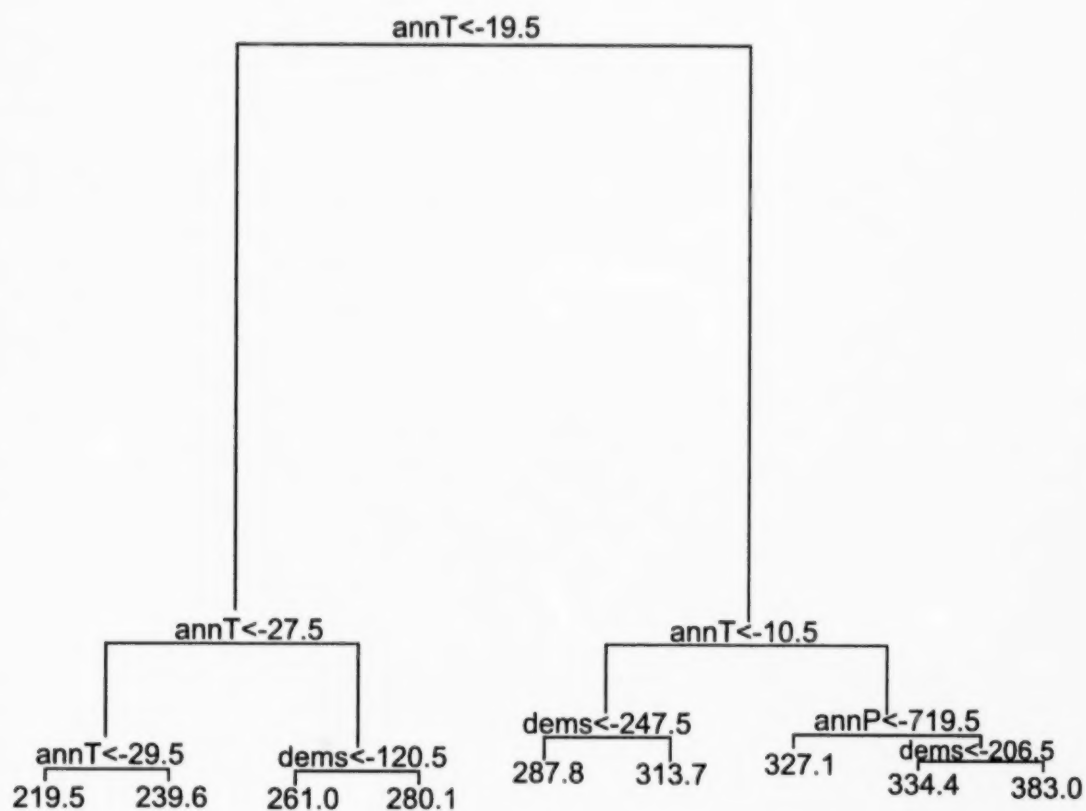


Figure 21a. Regression tree structures and labels of ecoregions and ecodistricts within Ecoprovince 1.

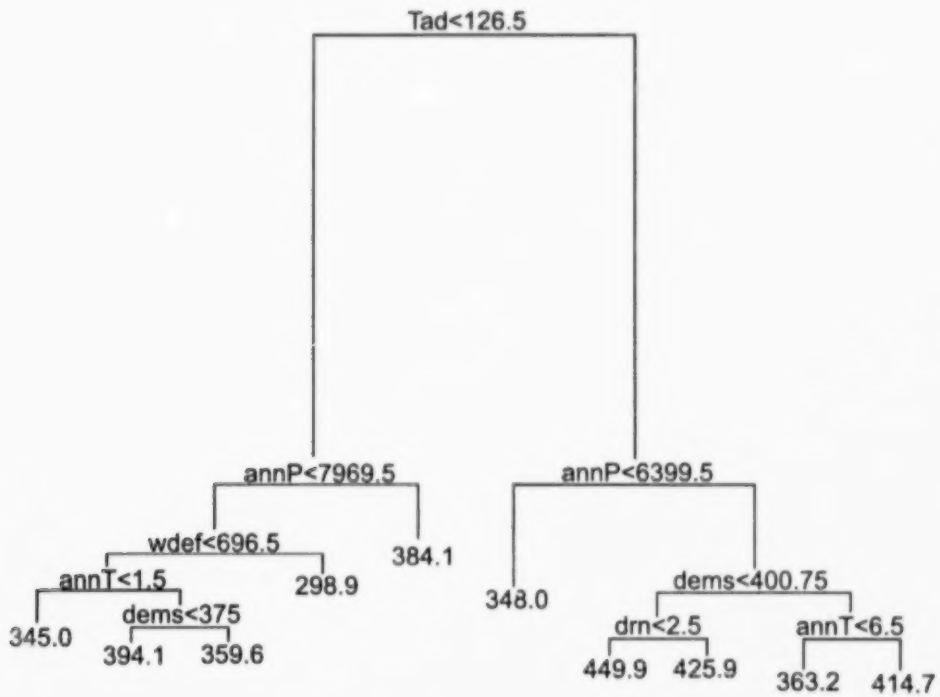


Figure 21b. Regression tree structures and labels of ecoregions and ecodistricts within Ecoprovince 2.

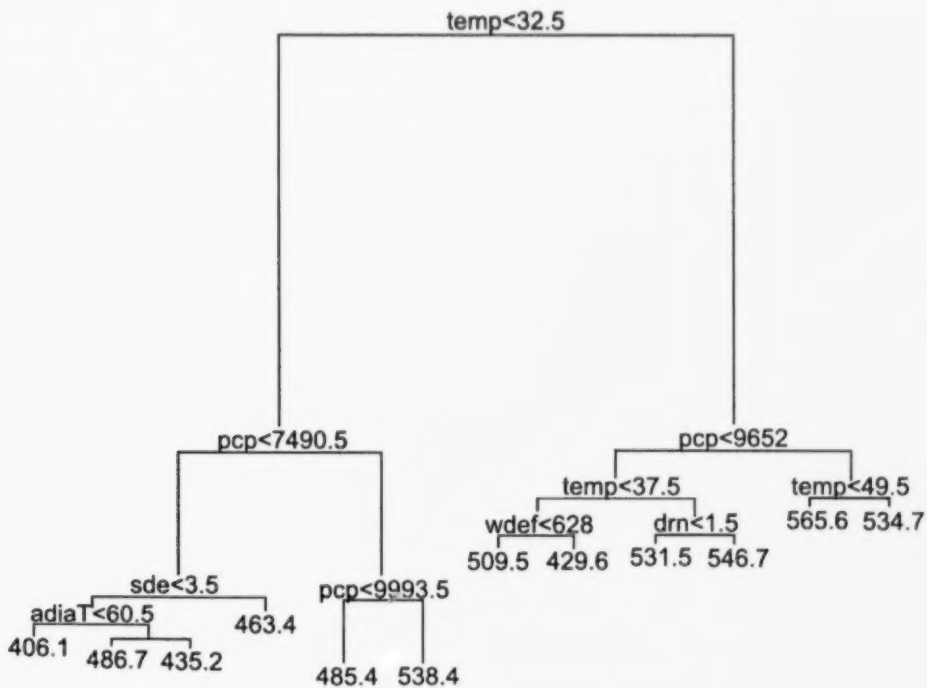


Figure 21c. Regression tree structures and labels of ecoregions and ecodistricts within Ecoprovince 3.

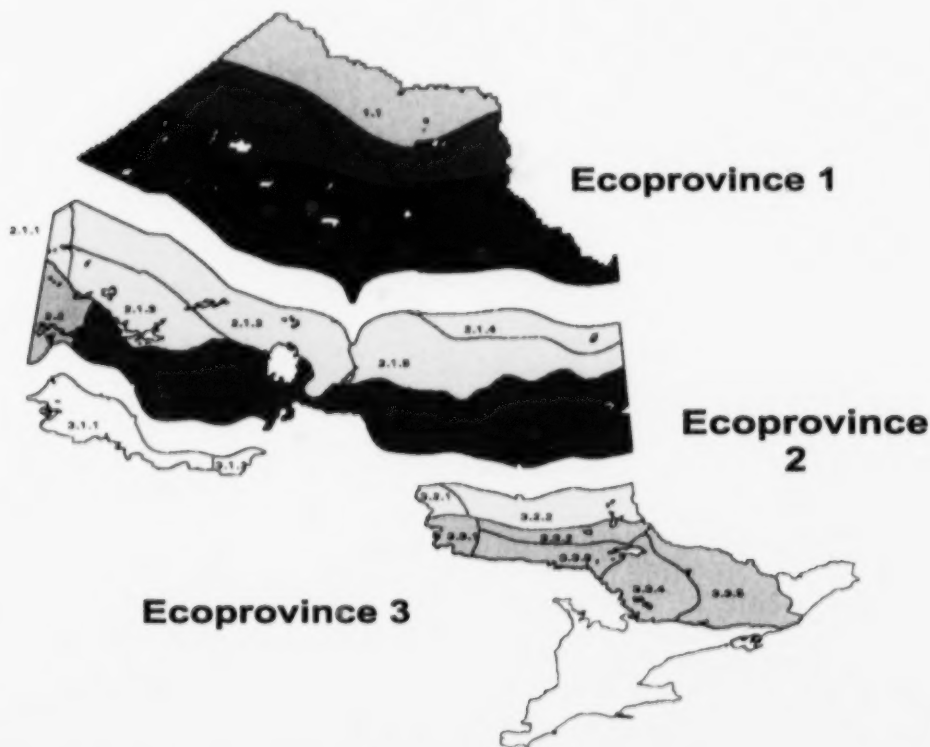


Figure 22. Map of the ecoregionalization of Ontario down to the Ecodistrict level.

Extensions to ecodistricts

As we constructed regression trees within each of the ecoprovinces (Figures 21a,b,c) to partition down to ecodistricts, more local terrain and substrate variables (adiabatically adjusted temperature, elevation, and soil drainage) began to control variation of forest ecosystem productivity. In these tree structures, ecoprovinces 1, 2, and 3 represent the northern, middle, and southern ecoprovinces, respectively. Ecoregions are numbered first with the parent ecoprovince number, followed by 1 or 2 to signify a "left" or "right" turn at each vertex of the regression tree, following the complete path down the tree to the ecoregion. Thus, the number of digits corresponds to the depth of the ecoregion within the tree. Ecodistricts are numbered sequentially with the number of the parent ecoregion, followed by a unique numerical identifier. Ecodistricts may not occupy unique positions within the regression tree thus they are not numbered. At this level, and with

the data sets used for these variables, areas of similar multivariate combinations of productivity and the terrain and substrate variables become spatially intermixed, thus 1 leaf in the regression tree may correspond to more than 1 contiguous region. Boundaries that correspond to more localized variables of elevation, soil drainage, and adiabatic temperature show greater spatial detail than the ecoregional and ecoprovincial boundaries. The relative strength and sharpness of these boundaries depends on the controlling variables: Climate variables show greater gradation while soil variables show gradation according to how well boundaries and purity of soil polygons can be mapped. Finally, Figure 22 shows the ecoregionalization from these regression trees transferred back to the map of Ontario, and down to the level of ecodistricts with the numbering scheme from Figure 21.



DISCUSSION

This investigation used the latest landscape ecology technology to generate an estimate of forest ecosystem productivity over the full province, analyze the spatial patterns and scales of variation of the forest productivity relative to a set of simple abiotic predictor variables, and generate the top levels of a hierarchical regionalization of the province. Primary forest ecosystem productivity was estimated using a landscape-level simulation of forest water and carbon budgets, which are used to calibrate satellite observations of ecosystem activity. This investigation used the productivity patterns for just the first available year of Pathfinder data (1987) but further analysis will investigate interannual variability to see if spatial patterns of productivity shift either from year to year or over the full range of Pathfinder data (1981-1994).

The productivity surface can be used to produce a hierarchical ecosystem regionalization of Ontario. An advantage of this approach is that a common, basic ecosystem variable is used as a common currency to quantify ecosystem function and process, avoiding some of the problems of using subjective and varying criteria for subdividing the province into ecounits. A relatively simple set of mean annual climatic variables and topographic variables can explain much of the spatial variation of ecosystem productivity at long length scales and large spatial scales of ecoprovinces and ecoregions and can extend down to the ecodistrict level. In addition, the quadtree analysis revealed that with details of the landscape at lower levels of the HEF hierarchy, higher-resolution data are increasingly required to explain the 8-km Pathfinder generated productivity estimates. Extending below the ecodistrict level would require higher-resolution information than was available for the present analysis (probably local plot data, e.g., FEC).

The nested ecoregionalization here is intriguing in its similarities and differences to more commonly used classification systems (e.g., Hills). An advantage of the current method is that the rules underlying the partitioning of each hierarchical level and each leaf are both explicit and variable for different parts of the province, reflecting the nested and spatially heterogeneous controls of ecosystem activity. In general, the technique is designed to identify distinct regions according to the multivariate control of a set of environmental variables on forest ecosystem productivity. The boundaries may be very gradational depending on the gradients of the controlling variables and the level of uncertainty in the spatial data sets. Thus, the precise location of the boundaries can be adjusted based on policy or management issues or the acquisition of more precise spatial data.

The quadtree analysis also shows much promise as a tool to map ecosystem variance as a prime attribute. An unambiguous measure of landscape heterogeneity can be derived by setting threshold variance(s) as the stopping criteria and analyzing the depth of decomposition. An index indicating landscape heterogeneity in ecosystem productivity or a set of other biophysical variables will be necessary in setting policy and planning management activities. Such information would be used to assess the variability in ecosystem response within given regions or districts, which may be just as important as the mean or expected response.

In addition, as OMNR and other resource agencies constantly need to streamline and improve the efficiency of data collection in addition to processing and disseminating information, the quadtree analysis can be used to allocate resources to spatially variable sampling densities required to estimate ecosystem variables. As the tree is decomposed to uniform sample variance, the sample density required to estimate statistical measures of ecosystem processes or composition related to

productivity is a direct function of the level of quadtree decomposition. However, the results of the quadtree analysis show that not all variables scale in the same manner, even if they are statistically related. Therefore, the spatial analysis methods used here should be repeated using a variety of other ecosystem biotic and abiotic variables.

Finally, we have chosen ecosystem productivity as a basic currency for comparing different ecosystems in the province and understanding ecosystem function and distribution to organize ecological variation. Such organization provides a means of planning resource management activities within spatial boundaries of similar ecological variation. While autotrophic terrestrial productivity can be considered a fundamental "enabling" ecological variable, as it provides the base of the terrestrial trophic web, other ecosystem variables that more directly suit a given policy or management issue could be chosen and used in a similar analysis. For example, issues related to water supply, flooding, or other hydrological variables would be better served by estimating the distribution of runoff production or evapotranspiration over the province. Watershed export of selected nutrients (e.g., DOC, NO₃) could be used as a variable in an analysis of terrestrial ecosystem impacts on aquatic ecosystems, while species abundance or related variables could be used for an analysis of forest community or biodiversity.

As not all variables will scale similarly, we must develop and maintain analytical methods using advanced information technologies that are flexible in application. Thus, the analyses carried out for this project are a prototype and illustration of an information-processing technology that could find a wider range of applications within the natural resources sector.

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(0.4 k P.R., 99 07 31)
ISSN 0381-3924
ISBN 0-7778-8796-7